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Review

State of the Art on the Interaction of Entomopathogenic Nematodes and Plant Growth-Promoting Rhizobacteria to Innovate a Sustainable Plant Health Product

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Abstract

Insect pests cause severe damage and yield losses to many agricultural crops globally. The use of chemical pesticides on agricultural crops is not recommended because of their toxic effects on the environment and consumers. In addition, pesticide toxicity reduces soil fertility, poisons ground waters, and is hazardous to soil biota. Therefore, applications of entomopathogenic nematodes (EPNs) and plant growth-promoting rhizobacteria (PGPR) are an alternative, eco-friendly solution to chemical pesticides and mineral-based fertilizers to enhance plant health and promote sustainable food security. This review focuses on the biological and ecological aspects of these organisms while also highlighting the practical application of molecular communication approaches in developing a novel plant health product. This insight will support this innovative approach that combines PGPR and EPNs for sustainable crop production. Several studies have reported positive interactions between nematodes and bacteria. Although the combined presence of both organisms has been shown to promote plant growth, the molecular interactions between them are still under investigation. Integrating molecular communication studies in the development of a new product could help in understanding their relationships and, in turn, support the combination of these organisms into a single plant health product.

Keywords: biological control; biofertilizer; EPN; PGPR; entomopathogenic nematodes; plant growth-promoting rhizobacteria; molecular communication; alginate formulation; crop protection; sustainable crop production

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1. Introduction

The increased use of chemical pesticides and mineral fertilizers in agriculture poses risks to human health, the environment, and soil microbiota. In addition, they disrupt the balance of the soil ecosystem. We propose the use of entomopathogenic nematodes (EPNs) and plant growth-promoting rhizobacteria (PGPR) as sustainable alternatives to chemical pesticides and mineral fertilizers, offering both insect pest control and enhanced plant growth. EPNs are effective in managing economically important insect pests [1]. Their application, often in combination with other crop protection products, has been well documented, highlighting their compatibility with a broad range of agricultural

equipment [1–3]. Similarly, PGPR enhance plant growth by improving nutrient availability, stimulating root development, and inducing systemic resistance against pests and diseases [4–6]. PGPR, particularly *Pseudomonas* spp., have been reported as promising biological control agents and biofertilizers due to their dual roles in promoting plant growth and suppressing insect pests. Their interactions with EPNs of the genus *Steinernema* have recently been pointed out as a major research area of interest for soil pest management [7].

Several research studies illustrated the compatibility between PGPR and EPNs. Some *Pseudomonas* strains have been shown to coexist with nematodes without affecting their life cycle [8,9]. Other *Pseudomonas* strains have been found to be associated with nematode infective juveniles (IJs) [10,11]. This coexistence and association address their potential role in enhancing host infection and nematode survival. Another study highlighted the synergistic interaction between *P. chlororaphis* and *S. feltiae*, resulting in enhanced efficacy against the cabbage root fly compared to individual treatments [7]. Although a synergistic relationship between the biological control agents has been reported, further research is needed to fully explore the mechanisms underlying this relationship.

A significant challenge in the practical applications of EPNs is their susceptibility to desiccation, UV radiation, and temperature changes, which severely impact their survival and infectivity during storage and application. Similarly, maintaining the viability and functional stability of bacterial inocula is essential for their effectiveness in promoting plant growth. Therefore, developing a suitable formulation for co-encapsulating EPNs and PGPR is important to maintain their biological activity during storage and enable reliable performance upon-application. A research study demonstrated the compatibility between *S. feltiae* and *P. ogarae*, providing evidence to support the feasibility of developing alginate formulations containing both organisms [12]. Successful colonization of the nematode IJs by the bacteria, both on the EPN cuticle and within their intestines, was demonstrated, ensuring that *P. ogarae* remained viable and effectively delivered into the soil. This indicates that IJs can play a critical role in releasing bacteria from such alginate formulations, with effective distribution in the rhizosphere.

Despite the well-documented benefits of EPNs and PGPR as individual biological agents, no experimental research has combined these two organisms into a single plant health product. This raises a significant research gap in the field of sustainable agriculture. One major challenge in combining the two agents is that the biological and physiological requirements of the organisms differ, especially in terms of moisture, oxygen, temperature, and nutrition. These differences make the co-encapsulation methodology challenging and require intensive effort to optimize methods, ensuring their viability, compatibility, and efficacy in co-delivery systems. Due to these difficulties, current practices continue to apply these biological organisms separately, increasing costs, labor, and logistical complexity in agricultural operations. Moreover, comparative genomic studies have revealed a sequence similarity between the fluorescent insecticidal toxin (*fit*) gene cluster of *Pseudomonas* spp. and the caterpillar's floppy (*mcf*) genes in EPN symbiont bacteria [11,13]. These shared sequences suggest a convergent or parallel evolutionary profile for insect pathogenesis. However, this molecular similarity has not been explored as a foundation for developing synergistic biocontrol products or co-formulations that take advantage of potential functional complementarity between EPNs and PGPR. To the best of our knowledge, no studies have investigated whether such genetic convergence could enhance their cooperative performance in pest control when co-applied. Additionally, very limited research has investigated the potential to exploit the biofertilizing capabilities of PGPR to promote plant growth alongside EPNs in a combined application. Furthermore, there is no research addressing the practical benefits of developing a plant health product containing nematodes and bacteria that will reduce the number of agricultural applications. Developing such a product with all these features will represent transformative

innovation in biological control, offering a multifunctional, cost-effective, and environmentally friendly alternative to chemical inputs.

Molecular communication is a promising interdisciplinary field, with extensive applications in human research, including targeted drug delivery, disease diagnostics, and synthetic biology [14]. Its integration into biological control and agricultural research remains extremely limited. Until now, the majority of molecular communication studies have been developed theoretically, relying on computational simulations with minimal biological validation [14]. Current research studies have achieved significant progress in modeling nanoscale communication systems; however, there remains a critical gap in applying these models to realistic biological settings, especially those involving interactions between soil organisms. The lack of translation of this research work limits our ability to understand and optimize interspecies interactions that are essential for effective biological control. Regarding plant health, nematodes and bacteria are two well-known biocontrol agents whose natural coexistence and synergistic interaction have been investigated recently without disrupting each other's core biological functions. This makes them suitable candidates for studying interspecies molecular communication theoretically by modeling their interactions and validating their molecular communication pathways in *in vitro* and *in vivo* experimental settings.

The present review aimed to provide a comprehensive overview of the development of alginate-based formulations that combine EPNs and PGPR as an integrated plant health product for sustainable pest management and enhanced plant health. This review highlighted the use of bioagents in biological control strategies and explored the natural biological interactions between them. Furthermore, this study evaluated the literature on alginate-based formulation approaches for both organisms, summarizing the encapsulating principles and bioagent performance upon applications. The genetic similarity between the insecticidal genes of nematodes and bacteria was introduced, which could serve as a molecular basis for enhancing the cooperative efficacy in pest control when co-applying both bioagents. This review also introduced molecular communication research as a multidisciplinary system adapted from telecommunications and biomedical sciences to model the signaling interactions between nematodes, bacteria, insects, and plants. We aimed to introduce molecular communication as an interdisciplinary avenue for exploring interactions between biological organisms, leading to insights into such relationships that can support the optimization of an EPN-PGPR co-formulation.

2. The Role of Soil Organisms in Sustainable Agriculture

Insects constitute a major threat to the production of vegetables and economically important crops worldwide. Significant yield losses are caused by larvae that feed on plant roots, which disrupts nutrient and water uptake, negatively affecting plant growth and subsequently leading to plant death [15–19]. Biological control agents, particularly soil-dwelling microorganisms that naturally inhabit the rhizosphere, offer a promising solution. These soil organisms have several levels of interactions with plants and play beneficial roles in crop production. Among these, EPNs and PGPR have shown great potential in managing insect pests and enhancing plant disease resistance [2]. EPNs are insect-parasitic nematodes that act as biocontrol agents against many insect pests. Their effectiveness against major insect pests and safe use make them ideal for integrated pest management programs [20]. Meanwhile, PGPR contribute to plant health by promoting root development, enhancing nutrient uptake, and activating the plant immune system. Plants can recognize these beneficial bacteria and respond by stimulating phytohormones and defensive metabolic pathways, resulting in induced systemic resistance without compromising plant growth or yield [2].

Enhancing plant health using soil biological agents aligns with several United Nations Sustainable Development Goals (UNSDGs), including Goal 2 (Zero Hunger), by increasing crop production and ensuring food security, Goal 3 (Good Health and Well-being), by reducing human exposure to hazardous pesticides, and Goal 6 (Clean Water and Sanitation), by reducing chemical runoff into aquatic systems. Moreover, these practices support Goal 14 (Life Below Water) and Goal 15 (Life on Land) by conserving biodiversity and enhancing soil health [21]. Healthy crops foster more nutritious food production and positively impact public health [22]. By decreasing the use of synthetic pesticides and mineral fertilizers, which disrupt soil microbiota and cause environmental damage, soil biological agents support soil ecosystems. This, in turn, enhances plant resilience and contributes to the development of sustainable agricultural systems that ensure food security and keep environmental integrity for future generations [23].

2.1. The Use of EPNs in Biological Control

EPNs are a diverse group of biological control agents with a broad host range that has been reported to infect over 200 insect pests [24,25]. EPNs of the family Steinernematidae have widespread uses as biological control agents for several important below- and above-ground insect pests [1,26]. The mode of insecticidal action of these nematodes relies on their symbiotic bacteria of the genus *Xenorhabdus*, which display high toxicity to insects and suppress the insect immune response. The non-feeding IJ is the third larval stage and the only stage able to survive outside the host. These non-feeding IJs carry their symbiotic bacteria and actively search for suitable insect hosts. They enter the host hemocoel through natural openings, such as the mouth, spiracles, and anus, and they can also penetrate the cuticle [27]. Once the IJs are inside the host, they release the symbiont bacteria, which proliferate rapidly, killing the insect within 24–48 h [28].

EPNs have exhibited significant activity as biocontrol agents. Nematodes of the family Steinernematidae have been considered as one of the best biocontrol agents of cabbage root fly (*Delia radicum*). Greenhouse experiments have also shown that nematodes were able to disrupt larvae before plant infestation [29–31]. More studies have illustrated that the efficacy of nematodes at specific dosages was promising, and they persisted in the soil for long periods, which kept the cabbage root fly population below the economic damage [32,33]. Different species of nematodes, namely, *S. feltiae*, *S. riobrave*, *S. carpocapsae*, *S. rarum*, and *S. glaseri*, were shown to be virulent against the larval stage of fruit flies *Bactrocera zonata* and *B. dorsalis* under laboratory, greenhouse, and field treatments [20]. In addition, *S. feltiae* showed a significant reduction in the larval stage of potato cutworm *Agrotis deprivata* [34]. According to the review conducted by Hoarao et al. [35], several *Steinernema* spp. have been used to control crucifer flea beetle adults in the USA and Japan in canola [36,37] and oilseed rape fields [38], respectively, and strip flea beetle adults in canola fields in China [39].

2.2. The Use of PGPR in Biological Control and Sustainable Agriculture

PGPR represent a vast variety of beneficial soil bacteria comprising over 21 genera and 47 species. *Pseudomonas* and *Bacillus* have been widely studied for their role in plant health [40]. Several PGPR species have shown great success in improving plant growth and fitness under various environmental conditions. They support plant health in several ways: improved nutrient absorption, nitrogen fixation, phosphate solubilization, production of phytosiderophores, and modulation of phytohormones [4,5,41]. Bacteria can modify phytohormone levels, in particular, salicylic acid, which is involved in the plant response to insects and pathogens by activating plant immune-related signaling pathways. They additionally secrete antimicrobial compounds and degrading enzymes that enhance plant defense by inducing systemic resistance (ISR) and, in some cases, induce systemic

acquired resistance (SAR) [42,43]. Some *P. fluorescens* strains synthesize the biochemical compound 2,4-diacetyl phloroglucinol (DAPG), which is directly involved in ISR in plants [44–54]. These diverse roles make bacteria very beneficial as biofertilizers and biopesticides in sustainable agriculture [41,45,49,54–57]. Moreover, genomic studies have reported their extended ecological versatility, making the bacteria core model organisms for understanding soil microbial ecology [58].

Several *P. fluorescens* strains have been studied, including *P. fluorescens*, *P. protegens*, *P. chlororaphis*, and *P. brassicacearum*, which colonized plant roots and competed for space and nutrients with soil-borne pathogens and protected the plants from pathogen attacks [59,60]. *P. fluorescens* strains have been reported to produce a range of antibacterial compounds and secondary metabolites, such as hydrogen cyanide (HCN), pyoluteorin, toxoflavin, orfamide A, DAPG, pyrrolnitrin, toxoflavin, and orfamide A [51,53]. In addition, they synthesize several enzymes, including chitinases and proteases. All these bioactive molecules were involved in inhibition or toxic actions against invertebrate pests [51,53]. *P. fluorescens* strains have been used as biological control agents against the pathogenic wheat fungus *Gaeumannomyces graminis* var. *tritic* [61]. As reported in Ramamoorthy et al. [50], *P. fluorescens* strains mediated ISR against several soil-borne pathogens of the sheath blight disease *Rhizoctonia solani*, halo blight disease *P. syringae* pv. *Phaseolicola*, and cucumber mosaic virus. Moreover, *P. fluorescens* strains mediated ISR against lepidopteran insect pests and influenced their growth and all development stages [50].

2.3. Shared Genetic Information Between EPNs and PGPR

Genomic analysis of *P. protegens* and *P. chlororaphis* indicated the presence of a genomic region encoding insecticidal genes, which are correlated with high insect toxicity involved in suppressing the insect immune response [13,62,63]. This insecticidal toxin, named fluorescent insecticidal toxin (fit), is expressed from a complex gene cluster located at the variable regions of the genome, with a substantial presence or absence of polymorphism [13,64,65]. Moreover, the *fit* gene cluster has a specific pattern and is not present in all *Pseudomonas* spp. As described, the complex *fit* gene cluster contains eight genes, which are *fitABCDEFGH*; each gene has a major function in insect mortality, toxin export, and toxic gene regulation. Furthermore, the *fitD* gene is flanked upstream by the *fitABC* genes and downstream by the *fitE* gene, encoding for components of a type I secretion system. The *fitD* gene encodes a high-molecular-weight protein, which is correlated with strong insecticidal activity. The *fitFGH* genes regulate toxin production, and the *fitF* gene is a sensor histidine kinase-response regulator hybrid, while the *fitH* gene and the *fitG* gene work on activating the insecticidal toxin expression [13,63]. The *fit* gene cluster has been found to cause rapid disruption of the insect midgut epithelium and hemocytes through activation of a BH-3-like apoptosis control domain [13]. Importantly, fit-derived toxins display high toxicity against insects; however, the detailed molecular mechanisms underlying their interaction with insect cells are still under investigation [11,53].

Comparative analysis of the *fit* complex gene cluster has shown similarity with the insecticidal gene named makes caterpillars floppy (*mcf*), produced by the nematode symbionts *Photorhabdus* and *Xenorhabdus* (see Figure 1) [13,62,63,66]. Several transposable elements were found in the *fit*/*mcf* gene cluster. A study carried out by Ruffner et al. [13] identified that the *fit* gene cluster of *P. protegens* and *P. chlororaphis* shares 73% identity with the caterpillar floppy insecticidal gene *mcf1* and 67% with the caterpillar floppy insecticidal gene *mcf*2. Investigating the genetic similarity between the insecticidal genes of those *Pseudomonas* spp. and the nematode symbiont bacteria could provide more insights into their molecular interaction between EPNs and PGPR. These findings are highly relevant for future research studies and will advance our understanding of the phylogenetic relation and evolution among these bioagents [10,11].

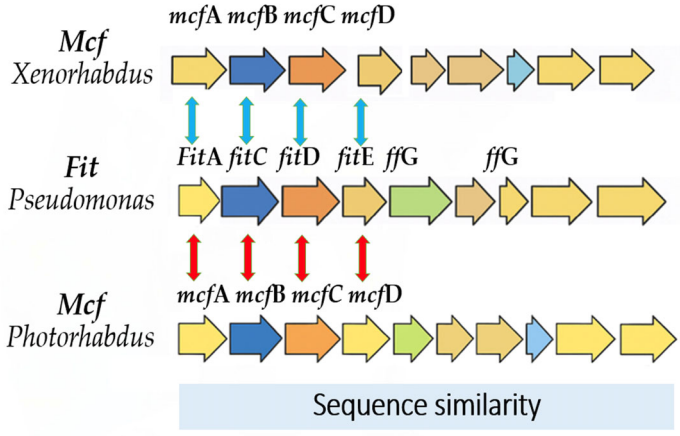

Figure 1. Comparative genomic organization of insecticidal gene clusters presenting the sequence similarity between *mcf* motifs in *Xenorhabdus* spp. and *Photorhabdus* spp. and *fit* motifs in *Pseudomonas* spp. Conserved regions are indicated with forward arrows in each gene cluster. Similiral first four forward arrows are showing homologous sequences between them. Vertical two ways blue arrows indicate regions of sequence similarity between *Pseudomonas* spp. (*fit*) and *Xenorhabdus* spp. (*mcf*), while Vertical two ways red arrows represent similarity between *Pseudomonas* spp. and *Photorhabdus* spp.

3. EPNs and Their Microbial Interactions

Several beneficial interactions have been discovered in the rhizosphere between soil-living microorganisms. Studies conducted by Ogier et al. [10] and Aujoulat et al. [67] reported the presence of Frequently Associated Microbiota (FAM) associated with nematodes and their core symbiont bacteria. The presence of FAM within nematode IJs can be attributed to their development, which occurs inside the insect host. As the IJs emerge from the insect cadaver, they have already been in contact with FAM before subsequently infecting a new host. FAM include PGPR, which are noncore bacteria isolated from nematode bodies. Molecular studies have revealed that PGPR play an important role in the parasitic lifecycle and the virulence of nematodes by producing antibacterial compounds involved in insect mortality [10,67]. For example, the genome of *P. fluorescens* strains harbors a virulence gene, which plays an essential role in suppressing the insect immune system [53,68]. A study carried out by Flury et al. [68] further demonstrated that certain PGPR groups can switch their lifestyle role to be either plant growth promoters or insecticides, adapting to their environment and modulating the secretion of antimicrobial compounds accordingly [63,66,69,70]. Furthermore, *Ochrobactrum* spp. showed the ability to tolerate insecticidal toxic compounds produced by the nematode symbiont *Photorhabdus luminescens* [67]. A unique interaction has also been observed between the nematode symbiont *P. luminescens* and microbes inhabiting plant roots, indicating potential rhizosphere adaptation and relationships with PGPR [71,72]. Researchers are still investigating how these symbiotic bacteria adapt in the rhizosphere and their relationship with PGPR.

Recent studies have confirmed the presence of *P. fluorescens* and *P. protegens* within nematode IJs [10,11], highlighting compatibility without affecting the nematode's life cycle or virulence. These bacteria are expected to play a role in host infection and nematode survival. Co-application of *Pseudomonas* spp. with nematodes has demonstrated synergistic effects and significantly increased insect mortality while maintaining nematode viability and infectivity [9,73]. Importantly, both *S. feltiae* SB 12 (1) and *P. ogarae* F113 *gfp* have shown a positive interaction under laboratory and greenhouse experiments, with no negative impact on the nematode survival, behavior, virulence, or bacterial root colonization [12]. Laboratory and greenhouse experiments revealed a positive interaction between these organisms, and a synergistic relationship was reported by the study. The bacteria

successfully colonized the nematode IJs and retained their ability to infect and kill *Galleria mellonella*. The bacteria were re-isolated from infected insect cadavers, confirming their persistence and involvement in the infection process. These results highlight the highly compatible and synergistic relationship between PGPR, nematodes, and their symbiotic bacteria, providing new insights into their ecological interactions and assisting future research into the molecular mechanisms that govern them.

Biological Interaction Between EPNs and PGPR

Soil is a dynamic environment where intricate communication networks occur between soil microbiomes. These interactions are mediated by biochemical molecules, which play an essential role in coordinating several functions, including root colonization, plant immune responses, and synergistic relationships [74,75]. Nematodes and bacteria interact with each other and with their hosts through the secretion of low-molecular-weight compounds, such as peptides, amino acids, volatile organic compounds, and phytohormones. These biomolecules activate signaling pathways that trigger extracellular and intracellular responses, promoting beneficial relationships that enhance plant health, improve nutrient uptake, and contribute to pest control [76].

According to Zwyssig et al. [9], a dynamic ecological relationship exists between *P. protegens*, *S. feltiae,* and its symbiont *X. bovienii*. This relationship is shaped by a synergistic and cooperative process that contributes to the successful infection and killing of the target insect. Both *P. protegens* and *X. bovienii* were found in insect hemolymph without any negative effects on the bacterial infection process or the virulence of the nematode. *A* mutualistic relationship occurs when *P. protegens* is able to access the insect body through the entry point created by the nematode during infection. Moreover, the presence of *P. protegens* and *S. feltiae*, along with their symbiont *X. bovienii*, within the insect body does not interfere with their natural lifestyle or infectivity with each other. These findings highlighted that the microbial interactions are highly dynamic depending on the nature of their relationship and the surrounding environmental conditions. While potential antagonistic interactions were expected in the study due to the production of antimicrobials by *P. protegens*, there was no evidence of substantial negative effects on the infectivity of the nematode. Although the *in vitro* experiments reported the ability of *P. protegens* to secrete antimicrobial compounds, such as DAPG and pyoluteorin, the *in vivo* experiments revealed that the activity of these compounds was either insufficient or did not impact nematode infectivity. This difference between *in vitro* and *in vivo* results could reflect the downregulation of antimicrobial biosynthesis genes in *P. protegens* upon interacting with the nematode and its symbiont bacteria. Similar results were observed in previous transcriptomic studies, highlighting the limited production of antimicrobial compounds under *in vivo* conditions [63]. These findings strongly support rejecting the hypothesis of antagonism between nematodes and bacteria, suggesting that both organisms can coexist within the same medium without compromising each other's ecological fitness.

A study carried out by Spescha et al. [7] presented a synergistic relationship among *Metarhizium brunneum*, *P. chlororaphis*, *S. feltiae*, and its symbiont bacteria, *X. bovienii*, for the management of *D. radicum.* In the study, the biocontrol agents were able to co-infect the insect host without showing antagonistic effects among each other. The compatibility among the three bioagents enabled them to colonize and establish in the insect simultaneously. *M. brunneum* facilitated initiating the infection by degrading the insect cuticle, thereby assisting the entry of the nematodes and the bacteria, while *P. chlororaphis* tended to dominate in the later stage of the infection process due to its strong antimicrobial properties. This finding highlighted that early colonization by fungi and nematodes created a favorable condition for bacterial expansion. Although the direct molecular interaction among the biological control agents was not investigated, the indirect interaction that

occurred via the host-mediated signals, such as host physiological changes or tissue breakdown induced by one bioagent, enhanced the performance of the other. The coexistence of the three bioagents inside the insect host, without them affecting each other's virulence, indicates effective ecological compatibility; each bioagent uses different resources or niches, thereby preventing direct competition.

By monitoring the behavior of the biological agents in greenhouse and field experiments, the authors reported that the nematodes and bacteria were able to colonize the rhizosphere without impacting their activity [7]. Although *P. chlororaphis* is known to secrete antimicrobial compounds that can inhibit bacterial growth, no harmful interaction was observed between *P. chlororaphis* and the nematode symbiont bacteria *X. bovienii.* The absence of negative interaction could be attributed to the altered metabolic activity of *P. chlororaphis* in a complex environment and reduced synthesis of antimicrobial compounds, which were insufficient to impact the activity of the symbiont bacteria *X. bovienii*, or the symbiont bacteria could have adopted resistance mechanisms against *P. chlororaphis*.

4. Molecular Communication Approaches

Enabled by the advance of synthetic biology, engineers are exploring the natural exchange in molecules at the micro/nanoscale using communications concepts, an approach named molecular communication, to investigate the biochemical status of cells (prokaryotic and eukaryotic) and to propose biotechnological applications for agricultural and health industries, such as the design of pollutant biosensors and a photosynthesis modulator [77–79]. In the early days of molecular communication, the designed models were based on the classical Shannon's communications model, which includes a transmitter, a propagation channel, a noise source, and a receiver, and these initial models enabled engineers to understand the challenges and opportunities for the development of communications systems at the micro/nanoscale [78]. For a molecular communication system, the transmitter is a natural/artificial cell that generates biochemical signals, representing the encoded information, to be propagated through a communication channel, often modeled as a diffusive medium. The noise source can represent the displacement of molecules while diffusing, the excess of biochemical signals in the propagating medium, or any effect that disrupts the effective reception of the transmitted molecular information by the receiver, which can be a similar or different species of the transmitter [14,80]. The receiver reacts biochemically based on the received information molecules [78]. Currently, these models have been further explored and expanded, resulting in novel methods to simulate and assess the communication performance in terms of molecular concentration arriving at the receiver or based on the receiver's detection accuracy [77]. These metrics form an engineering approach to measure the expected impact of molecular bioavailability on natural/artificial systems when they are performing tasks and interacting with other systems.

Natural communication signaling of living organisms is one of the main research interests in molecular communications [80]. For example, a biocompatibility communication system was developed to study bacterial and viral communication based on cell programming, which resulted in a viral attenuator that traps the Ebola virus from human blood [77]. For the application, synthetic biology and molecular communications were combined to develop a microfluidic device that exploits the chemical binding force between the Ebola virus and the engineered bacteria *Escherichia coli*. The authors demonstrated, through simulations, that the genetically engineered bacteria *E. coli* is able to bind virus particles in its cell membrane. Another example of modeling the natural signaling between organisms using molecular communications is the characterization of plant pheromone exchange. In this case, the authors of one study formulated an analytical model to describe all the stages of the communication process when plants exchange pheromones and evaluated the performance of their model based on variable parameters (e.g., wind

speed, diffusion constants, and distance) [81]. Similar principles can be applied to investigate the natural communication signaling between nematodes, bacteria, and hosts. In this context, a few communication models can be designed to represent the interactions that exist in EPN-PGPR systems. For example, an end-to-end communications system can be designed to model cooperative/competitive interactions between nematodes and bacteria, such as the ones described in Section Biological Interaction Between EPNs and PGPR. In this case, each organism can be represented as a transceiver (i.e., transmitter and receiver), the low-molecular-weight compounds are the information signal, and the environment where they are placed becomes the propagation channel (see Figure 2a). For this communications model, metrics, such as throughput (molecular concentration received over a period), the bit-error rate (ratio between the received noise and received information signal), and mutual information (measure of the receiver response based on the transmitted information signal), would be applied to analyze the system's performance (see Figure 2b). Furthermore, agent-based simulations could be performed to optimize the interaction and indicate possible avenues for enhancing/reducing the impact of the information signal's exchange [82].

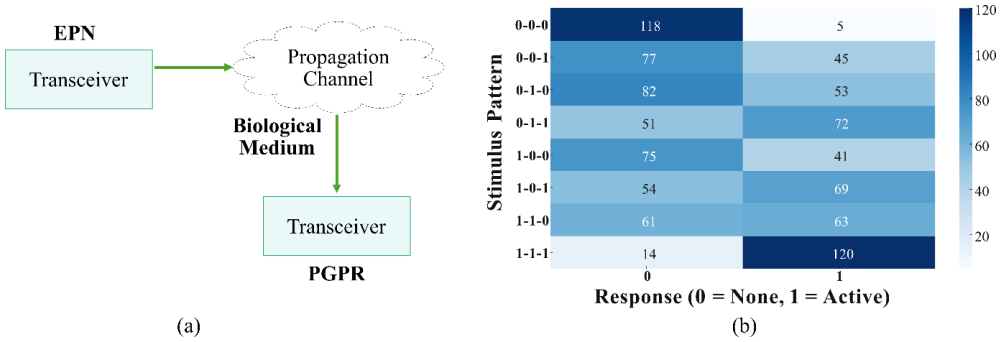

Figure 2. Molecular communication model and analysis of an EPN-PGPR interaction. (**a**) The proposed model is an end-to-end communications system, where the information signal leaves the EPNs and reaches the PGPR for processing and inducing changes in their behavior. (**b**) Mutual information analysis of the information signal received by the PGPR, considering a random emission of an information signal (with equal probabilities of sending "0" or "1") by three transmitters (EPNs) toward one receiver (PGPR). It can be noted that the likelihood of responding to stimuli increases with the number of transmitting EPNs. No noise was applied in this case.

Another communications model can be drawn from EPN-PGPR interactions to promote plant health when considering their influence on each other. In this case, a coherent feed-forward feedback loop (CFFL) network can be built using four actors: EPN (Node A), PGPR (Node B), plant (Node C), and insect (Node D). A CFFL network is also used to represent regulatory motifs where an upstream signal affects a downstream target through two parallel pathways. A direct path and an indirect path are connected by an intermediate node [83]. This two-pathway setup allows for signal processing by filtering out transient noise and establishing biological responses that are triggered in the presence of sustained input signals only. These characteristics make CFFLs a suitable approach in analyzing direct and indirect communication pathways between nematodes, bacteria, insects, and plants. In this network of nematodes, bacteria, insects, and plants, each biological component functions as a node, transmitting and receiving biochemical signals such as peptides, amino acids, and volatile organic compounds that coordinate their interactions and natural behaviors within the rhizosphere [84]. For example, plants can directly activate defensive signaling pathways in response to insect attacks while indirectly enhancing nematode and bacteria attraction by secreting volatile compounds [52,85]. A basic CFFL network in which the interactions between nodes affect the performance of the

system responses can be seen in Figure 3. Furthermore, by defining the weights based on the molecular exchange between the nodes, metrics such as PageRank (PR), Betweenness Centrality (BC), and Katz Centrality (KC) can be used to identify which node has higher influence on the whole network [86]. Also, by assuming that one of the nodes starts the communication process in this network, the consequent node activations (after receiving the information signal) are observed and used to evaluate the impact caused by the signal propagation within the network. Employing CFFL-based modeling on this natural molecular communication network can be a valuable tool for analyzing signal propagation, noise reduction, and how each component behaves as part of a complex biological network [87]. Nevertheless, please note that both molecular communication models represent novel ways to study complex biological networks, such as the one required to promote plant health.

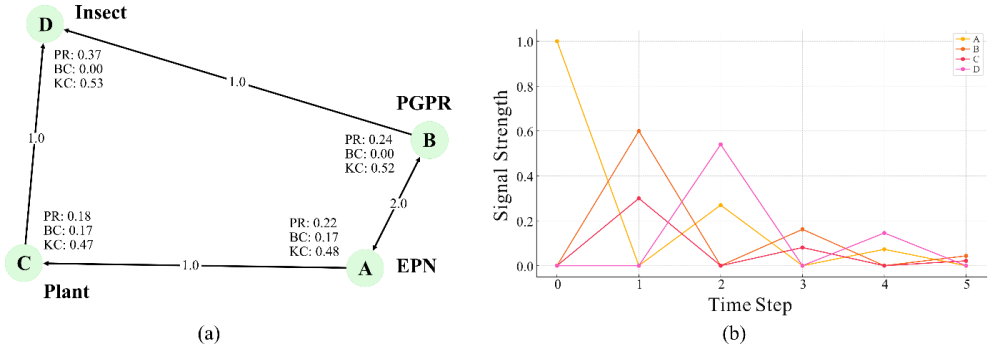

Figure 3. Molecular communication representation and analysis of a four-actor network: EPN, PGPR, plant, and insect. (**a**) For this example, the weight of the A to B interaction is considered twice that of the rest of the interactions. In this case, most of the information flow occurs in nodes A and C (high BC value), PageRank shows a greater importance of node D to the whole network, and nodes B and D show a relative degree of influence on the network (KC value). This can help to identify the impacts that a network can suffer when modifying the node behaviors. (**b**) Representation of the information signal propagation in this network, assuming that an information signal is propagated from node A. This metric can help identify the impact of possible delays (affecting the timing of node activation) and information signal attenuation (reducing its strength) on this CFFL network's molecular exchange.

5. Alginate-Based Formulations

Applying an alginate-based formulation means covering biological agents with a biopolymer layer that protects them against adverse conditions, such as desiccation, UV radiation, and temperature fluctuations, which significantly enhances their field efficacy [88–90]. Alginate is a linear polysaccharide of D-mannuronic and L-guluronic acids that is present in brown algae. The polysaccharide is most used in the encapsulation of nematodes and bacteria due to its unique properties, non-toxicity, biocompatibility, biodegradability, and water solubility [91–93]. These characteristics provide a protective environment that mitigates unfavorable conditions by maintaining hydration and shielding biological organisms from environmental stresses [49,93–97]. The alginate formulations are ideal for immobilizing biological agents and maintaining their viability and infectivity during storage and transport until field application [98–100]. In addition, when supplemented with additives or nanoparticles, alginate matrices show improved structural integrity without any negative impact on the encapsulated agents [101,102]. Furthermore, encapsulation in the alginate matrix allows for controlled and gradual release into the soil, enabling sustained interactions with the target plant or insect host. This method supports the long-term effectiveness of bioagents and is well aligned with environmentally sustainable agriculture goals [103]. The

use of alginate-based formulation is suitable for all types of agricultural equipment, allowing ease of application and flexibility. Considering these advantages, further development of an alginate formulation that combines biological agents within a single delivery system represents a reliable approach for future studies.

5.1. Alginate Formulation of EPNs

Some research studies have used alginate capsules in the encapsulation process of nematodes for the management of soil insect pests. A study conducted by Keya and Nelsen [104] was the first to utilize a capsule formulation of nematodes by adding an alginate solution containing nematode IJs into a calcium chloride solution. The encapsulation results were not promising because of unsuitable environmental conditions. Further improvements in encapsulation methods have been achieved to overcome the limitation of application conditions and to improve handling and enhance the shelf-life period. Several studies reported the efficacy of encapsulated nematodes in the management of underground insect pests. Calcium alginate capsules containing *Heterorhabditis bacteriophora* have been shown to protect maize against the western corn rootworm *Diabrotica virgifera* using a Trojan horse strategy. In the field and greenhouse experiments conducted by Hiltpold et al. [105], encapsulated *H. bacteriophora* nematodes successfully survived within the calcium alginate matrix and were able to emerge from the capsules under soil application. These encapsulated nematodes infected and killed the larvae. The study demonstrated that the capsule formulation contained attractants (root volatiles and CO_2) and a phagostimulant (corn root powder) that enhanced larvae attraction to the capsules. Capsules buried close to the maize roots showed less root damage and protected the plant roots compared to controls. The authors noted that *H. bacteriophora* IJs escaped from the alginate capsules after a few days of storage at room temperature. To prevent the nematode IJs from escaping from the alginate capsules during storage, the authors optimized the encapsulation process by reducing the gelling reaction temperature to 4°C and increasing the calcium chloride concentration used for cross-linking. These formulation adjustments resulted in the generation of more rigid and stable calcium alginate capsules. The produced capsules effectively maintained *H. bacteriophora* IJs without escape during storage for up to two weeks. The study highlighted that the improved capsule solidness and low temperature restricted IJ movement and metabolic activity. As a result, the shelf life of the encapsulated IJs increased while maintaining their viability and infectivity [106]. Further efforts have been made to improve the desiccation and UV tolerance of the alginate formulation used for encapsulating nematode IJs. In the study by Kim et al. [98], an optimized alginate formulation was developed using calcium alginate hydrogel beads containing *H. bacteriophora*. The alginate formula included 18% glycerol, which served as a hydrophilic additive to reduce water loss and the metabolic activity of the IJs, allowing them to preserve their viability and energy until application time. In addition, the capsules were developed to enhance mechanical strength and reduce UV damage. Field experiments demonstrated that this improved formulation significantly reduced root damage caused by *Dia. virgifera* in maize. The encapsulated nematodes remained viable for extended periods under storage at room temperature in the dark.

Laboratory experiments have been carried out to evaluate the efficacy of calcium alginate capsules containing *H. bacteriophora* in managing the banded cucumber beetle, *Dia. balteata* LeConte, in maize [107]. In the study, the encapsulated nematodes were introduced to the soil either simultaneously with or one week after the addition of *Dia. balteata* larvae to maize plants. The results showed that the application time significantly determined the final outcomes. When the encapsulated nematodes were applied one week after larvae infestation, the nematode treatment was ineffective: the plants had significant root damage, and a reduction in plant growth was observed. In contrast, when the

encapsulated nematodes were applied simultaneously with the larvae, the larvae's mortality increased, a significant reduction in root damage was observed, and enhanced plant performance was noted. These results highlight the importance of a synchronized application time for achieving effective pest control with encapsulated nematodes.

5.2. Alginate-Based Formulation of PGPR

An alginate-based bead formulation has been employed to encapsulate bacteria for several purposes. Encapsulated bacteria have been used to promote plant growth, as biofertilizers, and as biological control agents against plant pathogens and insect pest infections. Many research studies have been carried out on encapsulating *P. fluorescens* strains to manage plant pathogens; however, the use of alginate-based bacterial formulations for controlling insect pests is rarely reported. In one study, *P. fluorescens* strains were applied to wheat cultivated in non-sterile loamy sand soil [108]. The study demonstrated how bacterial cells were encapsulated in calcium alginate beads and applied to the rhizosphere of wheat plants grown in unsterilized loamy sand under controlled soil environments. One week after application, a significant population of viable *P. fluorescens* cells was detected on the plant root surfaces, showing successful release from the alginate beads and enabling efficient colonization of the rhizosphere. The study also highlighted that the encapsulated bacteria showed high rhizosphere competence, verifying the potential of the alginate formulation to support bacterial persistence and root colonization under greenhouse conditions. An *in vitro* study was conducted to determine the biological control capabilities of *P. fluorescens* F113 LacZY encapsulated in dry alginate microbeads for managing the soil-borne pathogens *Pythium ultimum* and *R. solani* in sugar beet [109]. According to the study, the encapsulated bacteria displayed high survival rates within the alginate formulation and retained their metabolic activity after rehydration. Following application, *P. fluorescens* F113 LacZY successfully colonized the root surfaces and significantly reduced fungal infections. The study highlighted that alginate microbeads could be used as a viable alginate formulation for introducing beneficial microorganisms into the soil. An alginate-based bead formulation was developed for coating crisphead lettuce seeds with *P. aeruginosa* LY-11 for the biological control of damping-off and bottom rot diseases caused by *R. solani*. In a study carried out by Heo et al. [110], lettuce seeds were coated with a calcium alginate solution formulated with *P. aeruginosa* LY-11 and subsequently dried before sowing. The results showed that the encapsulated bacteria maintained their viability and were released into the soil upon seed germination. Additionally, the bacteria successfully colonized the lettuce roots and significantly limited the disease incidence. Furthermore, the bacteria were able to induce systemic resistance in the lettuce plants, protecting them from bottom rot disease.

Microbeads were developed for encapsulating two strains of *P. fluorescens* (VUPF5 and T17-4) to control wilt disease in potatoes caused by *Fusarium solani*. According to Pour et al. [101], both *P. fluorescens* strains were encapsulated using a mixture of alginate and gelatin, enhanced with chitin and silicon dioxide nanoparticles to improve bead integrity and bacterial viability. The developed formulation contained the bacteria, which were applied to the soil under controlled greenhouse conditions. The study reported that the *P. fluorescens* strains significantly reduced disease severity and protected potato cultivation from *F. solani* infection. In addition, a significant increase in potato growth indicators, including fresh and dry weight, root length, shoot length, and root density, was observed.

Another study investigated the integration of alginate-based encapsulation with functional nanoparticles for enhancing rice seedling growth and disease resistance. In the study, *Pseudomonas* sp. DN18 was encapsulated in an alginate medium supplemented with nanoparticles of salicylic acid and zinc oxide. The authors reported that the addition of these nanoparticles improved the structural integrity and stability of the microbeads,

showed a synergistic antimicrobial effect, and enhanced plant growth. Field experiments showed promising results in suppressing the seedling blight pathogen *Sclerotium rolfsii*. Additionally, the treatment enhanced overall plant health [102]. *In vitro* and *in vivo* bioassays have been carried out to evaluate the storage stability, delivery efficiency, and bioremediation capability of *P. fluorescens* F113 encapsulated in alginate beads in soil contaminated with polychlorinated biphenyls (PCBs). A study by Power et al. [111] presented genetically modified strains of *P. fluorescens* F113 that were engineered for use in PCB degradation and biosensing. The bacteria were successfully encapsulated in calcium alginate micro-alginate beads and maintained their viability for up to six weeks at 4 °C. Upon application to contaminated soil, the encapsulated *P. fluorescens* F113 retained their degradative and biosensor activities, allowing them to detect and break down PCBs. The developed alginate formulation allowed for controlled release and localized containment of the bacteria, reducing environmental remediation.

6. Current Challenges, Research Barriers, and Future Directions

Although the promising potential of nematodes and bacteria as sustainable bioagents for pest control and plant enhancement exists, major challenges and research gaps limit their combination in a single product for use in practical agricultural systems. The critical challenge is the biological differences that arise from the distinct physiological requirements of both organisms. These include differences in moisture, oxygen, nutrients, and temperature tolerance, which require more effort in developing suitable co-formulations. The developed co-formulation should facilitate handling of the bioagents and support an efficient delivery system. The shelf life of the developed co-formulation is also essential for large-scale production to meet standard commercialization. Despite the alginate-based encapsulation approaches that have been developed and separately applied for both nematodes and bacteria, no study has been conducted on co-encapsulating them into a single stable and functional plant health product. The lack of a combined formulation is a major barrier to real-world implementation, as it necessitates redundant applications, increases input costs, and creates logistical complexity for all farmers. Comparative genomics showed high sequence similarity between the *fit* gene cluster in *Pseudomonas* spp. and the *mcf* insecticidal gene in nematode symbiont bacteria, suggesting a high chance for synergistic biocontrol performance. No research has focused on utilizing these shared molecular features to enhance cooperative pest control or the dual role of bacteria as biofertilizers.

The application of molecular communication research in agricultural sciences is still limited, despite its extensive use in human health research and nanoscale systems. The adaptation of molecular communication frameworks to soil ecosystems and biological compounds remains practically limited and represents a significant gap in both theory and application. The development of innovative, dynamic co-formulations supported by biologically validated models to simulate signaling and interaction among biological compounds remains speculative. Therefore, future research could focus on the following aspects: (1) Optimizing co-formulation technology, such as alginate-based formulation, to maintain bioagents' viability, compatibility, and functionality during storage and until application. This will ensure efficient delivery of both bioagents into the soil, offering sustained pest control and promoting plant growth over time. (2) Investigating the ecological and genetic perspectives underlying nematode and bacteria interactions, considering their insecticidal gene similarities, colonization behavior, and influence on insect hosts and plant health. (3) Establishing a new frontier in molecular communication modeling tailored to soil biological systems. The systems should go beyond theoretical simulations to incorporate experimental data from laboratory bioassays and greenhouse and field experiments. Eventually, overcoming these barriers will pave the way for novel plant health products that reduce the use of chemical pesticides and mineral-based fertilizers, enhance

agricultural applications, and contribute to sustainable crop production. Figure 4 represents the development of alginate-based encapsulated EPNs and PGPR for pest control and promoting plant growth.

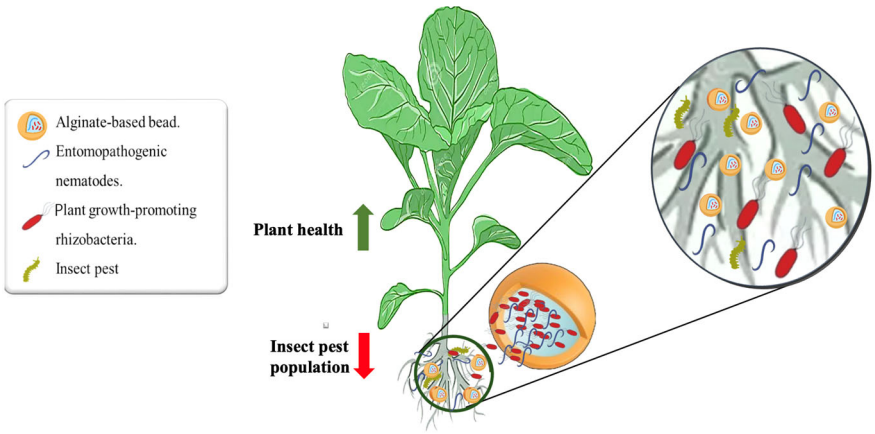

Figure 4. Schematic representation of alginate-based beads as a co-delivery system for EPNs and PGPR for pest control and plant growth promotion. Upon application, the biological agents will be released at the same time from the alginate formulation into the soil. Thereafter, nematodes will search for soil insects to infect and kill them. Simultaneously, PGPR colonize plant roots, enhancing nutrient uptake, stimulating root development, and, in some cases, inducing resistance against biotic and abiotic factors. This multifunctional strategy offers synergistic benefits through nematodes, providing effective pest control and bacteria supporting plant growth and resilience.

7. Conclusions

The integration of nematodes and bacteria into a single plant health product presents a novel and promising technology for sustainable crop production. This current review describes the complementary roles of nematodes and bacteria, where nematodes provide effective biological control against insect pests, and bacteria enhance plant health through nutrient mobilization and induced resistance. Although both bioagents have been individually applied in agriculture with great success, their combined application remains under investigation due to challenges in encapsulation compatibility and biological requirements. Advances in alginate-based formulations offer a promising foundation to co-deliver both organisms, overcoming existing barriers while maintaining their viability and efficacy. Co-encapsulating nematodes and bacteria into a single product can significantly reduce the number of agricultural applications, lower input costs, provide effective pest control through the nematodes, and enhance plant growth and resilience through the bacteria, addressing two critical agricultural sustainability needs simultaneously. Additionally, the genetic similarity between the insecticidal gene clusters of PGPR and the nematode symbiont bacteria indicates a potential role in enhancing cooperative performance and provides new ideas for molecular innovation in pest management. Furthermore, integrating molecular communication systems into biological control research will provide a unique framework to explore and modulate the interactions between nematodes and bacteria. These frameworks will simulate and predict signal transmission and functional coordination between biological components, paving the way for better optimization of the co-formulations.

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Abbreviations

The following abbreviations are used in this manuscript:

EPN	entomopathogenic nematodes
PGPR	plant growth-promoting rhizobacteria
IJs	infective juveniles
fit	fluorescent insecticidal toxin
Mcf	makes caterpillars floppy
DAPG	2,4-diacetyl phloroglucinol
FAM	Frequently Associated Microbiota
ISR	inducing systemic resistance
SAR	systemic acquired resistance
UV	Ultraviolet
HCN	hydrogen cyanide
PCBs	polychlorinated biphenyls
CFFLs	coherent feed-forward loops
UNSDGs	United Nations Sustainable Development Goals

References

1. Lacey, L.A.; Georgis, R. *Entomopathogenic nematodes* for Control of Insect Pests Above and Below Ground with Comments on Commercial Production. *J. Nematol.* **2012**, *44*, 218–225.
2. Koppenhöfer, A.M.; Shapiro-Ilan, D.I.; Hiltpold, I. *Entomopathogenic nematodes* in Sustainable Food Production. *Front. Sustain. Food Syst.* **2020**, *4*, 125. https://doi.org/10.3389/fsufs.2020.00125.
3. Shapiro-Ilan, D.; Dolinski, C. Entomopathogenic Nematode Application Technology. In *Nematode Pathogenesis of Insects and Other Pests: Ecology and Applied Technologies for Sustainable Plant and Crop Protection*; Campos-Herrera, R., Ed.; Springer International Publishing: Cham, Switzerland, 2015; pp. 231–254, ISBN 978-3-319-18266-7.
4. Massa, F.; Defez, R.; Bianco, C. Exploitation of Plant Growth Promoting Bacteria for Sustainable Agriculture: Hierarchical Approach to Link Laboratory and Field Experiments. *Microorganisms* **2022**, *10*, 865. https://doi.org/10.3390/microorganisms10050865.
5. Vejan, P.; Abdullah, R.; Khadiran, T.; Ismail, S.; Nasrulhaq Boyce, A. Role of Plant Growth Promoting Rhizobacteria in Agricultural Sustainability—A Review. *Molecules* **2016**, *21*, 573. https://doi.org/10.3390/molecules21050573.
6. Lugtenberg, B.; Kamilova, F. Plant-Growth-Promoting Rhizobacteria. *Annu. Rev. Microbiol.* **2009**, *63*, 541–556. https://doi.org/10.1146/annurev.micro.62.081307.162918.
7. Spescha, A.; Weibel, J.; Wyser, L.; Brunner, M.; Hess Hermida, M.; Moix, A.; Scheibler, F.; Guyer, A.; Campos-Herrera, R.; Grabenweger, G.; et al. Combining entomopathogenic Pseudomonas bacteria, nematodes and fungi for biological control of a belowground insect pest. *Agric. Ecosyst. Environ.* **2023**, *348*, 108414. https://doi.org/10.1016/j.agee.2023.108414.
8. Neidig, N.; Paul, R.J.; Scheu, S.; Jousset, A. Secondary Metabolites of *Pseudomonas fluorescens* CHA0 Drive Complex Non-Trophic Interactions with Bacterivorous Nematodes. *Microb. Ecol.* **2011**, *61*, 853–859. https://doi.org/10.1007/s00248-011-9821-z.
9. Zwyssig, M.; Spescha, A.; Patt, T.; Belosevic, A.; Machado, R.A.R.; Regaiolo, A.; Keel, C.; Maurhofer, M. Entomopathogenic pseudomonads can share an insect host with *Entomopathogenic nematodes* and their mutualistic bacteria. *ISME J.* **2024**, *18*, wrae028. https://doi.org/10.1093/ismejo/wrae028.
10. Ogier, J.-C.; Pagès, S.; Frayssinet, M.; Gaudriault, S. Entomopathogenic nematode-associated microbiota: From monoxenic paradigm to pathobiome. *Microbiome* **2020**, *8*, 25. https://doi.org/10.1186/s40168-020-00800-5.
11. Ruiu, L.; Marche, M.G.; Mura, M.E.; Tarasco, E. Involvement of a novel *Pseudomonas protegens* strain associated with entomopathogenic nematode infective juveniles in insect pathogenesis. *Pest Manag. Sci.* **2022**, *78*, 5437–5443. https://doi.org/10.1002/ps.7166.

12. Jo Hurley, M. An Investigation on the Interactions Between *Entomopathogenic nematodes* and Plant Growth Promoting Bacteria. Ph.D. Thesis, South East Technological University, Carlow, Ireland, 2018.
13. Ruffner, B.; Péchy-Tarr, M.; Höfte, M.; Bloemberg, G.; Grunder, J.; Keel, C.; Maurhofer, M. Evolutionary patchwork of an insecticidal toxin shared between plant-associated pseudomonads and the insect pathogens *Photorhabdus* and *Xenorhabdus*. *BMC Genom.* **2015**, *16*, 609. https://doi.org/10.1186/s12864-015-1763-2.
14. Farsad, N.; Yilmaz, H.B.; Eckford, A.; Chae, C.-B.; Guo, W. A Comprehensive Survey of Recent Advancements in Molecular Communication. *IEEE Commun. Surv. Tutor.* **2016**, *18*, 1887–1919. https://doi.org/10.1109/COMST.2016.2527741.
15. Gaffney, M.; Walsh, L.; Cucak, M.; Fealy, R.; Purvis, G.; Lambkin, K.; Griffin, D.; McNamara, L.; Thorne, F.; Fealy, R.; et al. Establishing a Platform for Integrated Pest Management in Irish Crops. *EMS Annual Meeting Abstracts*. 2017;14:1. Available online: https://meetingorganizer.copernicus.org/EMS2017/posters/25527 (accessed on 25 June 2025).
16. Oerke, E.-C. Crop losses to pests. *J. Agric. Sci.* **2006**, *144*, 31–43. https://doi.org/10.1017/S0021859605005708.
17. Ofuya, T.I.; Okunlola, A.I.; Mbata, G.N. A Review of Insect Pest Management in Vegetabl e Crop Production in Nigeria. *Insects* **2023**, *14*, 111. https://doi.org/10.3390/insects14020111.
18. Ouaarous, M.; El Fakhouri, K.; Taarji, N.; Baouchi, A.; Amri, M.; Ramdani, C.; Sobeh, M.; Mesfioui, A.; El Bouhssini, M. Impact of Field Insect Pests on Seed and Nutritional Quality of Some Important Crops: A Comprehensive Review. *ACS Omega* **2025**, *10*, 8779–8792. https://doi.org/10.1021/acsomega.4c08982.
19. Tonnang, H.E.; Sokame, B.M.; Abdel-Rahman, E.M.; Dubois, T. Measuring and modelling crop yield losses due to invasive insect pests under climate change. *Curr. Opin. Insect Sci.* **2022**, *50*, 100873. https://doi.org/10.1016/j.cois.2022.100873.
20. Usman, M.; Wakil, W.; Shapiro-Ilan, D.I. *Entomopathogenic nematodes* as biological control agent against *Bactrocera zonata* and *Bactrocera dorsalis* (Diptera: Tephritidae). *Biol. Control* **2021**, *163*, 104706. https://doi.org/10.1016/j.biocontrol.2021.104706.
21. FAO. *Status of the World's Soil Resources: Main Report*; ITPS: Rome, Italy, 2015; ISBN 978-92-5-109004-6.
22. FAO. *Building Climate Resilience for Food Security and Nutrition*; WFP: Rome, Italy, 2018; ISBN 978-92-5-130571-3.
23. Imperiali, N.; Chiriboga, X.; Schlaeppi, K.; Fesselet, M.; Villacrés, D.; Jaffuel, G.; Bender, S.F.; Dennert, F.; Blanco-Pérez, R.; Van Der Heijden, M.G.A.; et al. Combined Field Inoculations of Pseudomonas Bacteria, Arbuscular Mycorrhizal Fungi, and *Entomopathogenic nematodes* and their Effects on Wheat Performance. *Front. Plant Sci.* **2017**, *8*, 1809. https://doi.org/10.3389/fpls.2017.01809.
24. Miles C, Blethen C.; Gaugler R.; Shapiro-Ilan D.; Murray T. Using entomopathogenic nematodes for crop insect pest control. *A Pacific Northwest Extension Publications (PNW 544)*. 2012, 1–9. Available online: https://www.researchgate.net/profile/Randy-Gaugler/publication/263444652_Using_beneficial_nematodes_for_crop_insect_pest_control/links/0046353ad890787049000000/Using-beneficial-nematodes-for-crop-insect-pest-control.pdf (accessed on 25 June 2025).
25. Lacey, L.A.; Grzywacz, D.; Shapiro-Ilan, D.I.; Frutos, R.; Brownbridge, M.; Goettel, M.S. Insect pathogens as biological control agents: Back to the future. *J. Invertebr. Pathol.* **2015**, *132*, 1–41. https://doi.org/10.1016/j.jip.2015.07.009.
26. Platt, T.; Stokwe, N.F.; Malan, A.P. A Review of the Potential Use of *Entomopathogenic nematodes* to Control Above-Ground Insect Pests in South Africa. *South Afr. J. Enol. Vitic.* **2020**, *41*, 1–16. https://doi.org/10.21548/41-1-2424.
27. Lewis, E.; Campbell, J.; Griffin, C.; Kaya, H.; Peters, A. Behavioral ecology of *Entomopathogenic nematodes*. *Biol. Control* **2006**, *38*, 66–79. https://doi.org/10.1016/j.biocontrol.2005.11.007.
28. Devi, G. Management of Cutworm by *Entomopathogenic nematodes*—A Review. *Int. J. Curr. Microbiol. Appl. Sci.* **2020**, *9*, 2520–2526. https://doi.org/10.20546/ijcmas.2020.906.306.
29. Hough-Goldstein, J.; Janis, J.A.; Ellers, C.D. Release Methods for *Perillus bioculatus* (F.), a Predator of the Colorado Potato Beetle. *Biol. Control* **1996**, *6*, 114–122. https://doi.org/10.1006/bcon.1996.0014.
30. Kapranas, A.; Sbaiti, I.; Degen, T.; Turlings, T.C.J. Biological control of cabbage fly *Delia radicum* with *Entomopathogenic nematodes*: Selecting the most effective nematode species and testing a novel application method. *Biol. Control* **2020**, *144*, 104212. https://doi.org/10.1016/j.biocontrol.2020.104212.
31. Palumbo, J.C.; Kerns, D.L.; Engle, C.E.; Sanchez, C.A.; Wilcox, M. lmidacloprid Formulation and Soil Placement Effects on Colonization by *Sweetpotato whitefly* (Homoptera: Aleyrodidae): Head Size and Incidence of Chlorosis in Lettuce. *J. Econ. Entomol.* **1996**, *89*, 735–742. https://doi.org/10.1093/jee/89.3.735.
32. Beck, B.; Spanoghe, P.; Moens, M.; Brusselman, E.; Temmerman, F.; Pollet, S.; Nuyttens, D. Improving the biocontrol potential of Steinernema feltiae against *Delia radicum* through dosage, application technique and timing. *Pest Manag. Sci.* **2014**, *70*, 841–851. https://doi.org/10.1002/ps.3628.
33. Triapitsyn, S.V. A key to the *Mymaridae* (Hymenoptera) egg parasitoids of *Proconiine sharpshooters* (Hemiptera: Cicadellidae) in the Nearctic region, with description of two new species of *Gonatocerus*. *Zootaxa* **2006**, *1203*, 1–38. https://doi.org/10.5281/zenodo.172335.

34. Lankin, G.; Castaneda-Alvarez, C.; Vidal-Retes, G.; Aballay, E. Biological control of the potato cutworm *Agrotis deprivata* (Lepidoptera: Noctuidae) with *Steinernema feltiae* LR (Nematoda: Steinernematidae): Influence of the temperature, host developmental stage, and application mode on its survival and infectivity. *Biol. Control* **2020**, *144*, 104219. https://doi.org/10.1016/j.biocontrol.2020.104219.
35. Hoarau, C.; Campbell, H.; Prince, G.; Chandler, D.; Pope, T. Biological control agents against the cabbage stem flea beetle in oilseed rape crops. *Biol. Control* **2022**, *167*, 104844. https://doi.org/10.1016/j.biocontrol.2022.104844.
36. Hokkanen, H.M.T. Biological control methods of pest insects in oilseed rape. *EPPO Bull.* **2008**, *38*, 104–109. https://doi.org/10.1111/j.1365-2338.2008.01191.x.
37. Shapiro-Ilan, D.; Hazir, S.; Glazer, I. Chapter 6—Basic and Applied Research: *Entomopathogenic nematodes*. In *Microbial Control of Insect and Mite Pests*; Lacey, L.A., Ed.; Academic Press: Cambridge, MA, USA, 2017; pp. 91–105, ISBN 978-0-12-803527-6.
38. Srce, S. Računski Centar—Effectiveness of *Entomopathogenic nematodes* in the Control of Oilseed Rape Pests. Available online: https://www.croris.hr/crosbi/publikacija/prilog-skup/860354?utm_source=chatgpt.com (accessed on 25 June 2025).
39. Xu, C.; De Clercq, P.; Moens, M.; Chen, S.; Han, R. Efficacy of *Entomopathogenic nematodes* (Rhabditida: Steinernematidae and Heterorhabditidae) against the striped flea beetle, *Phyllotreta striolata*. *BioControl* **2010**, *55*, 789–797. https://doi.org/10.1007/s10526-010-9300-3.
40. Kim, W.-I.; Cho, W.K.; Kim, S.-N.; Chu, H.; Ryu, K.-Y.; Yun, J.-C.; Park, C.-S. Genetic Diversity of Cultivable Plant Growth-Promoting Rhizobacteria in Korea. *J. Microbiol. Biotechnol.* **2011**, *21*, 777–790. https://doi.org/10.4014/jmb.1101.01031.
41. Bhattacharyya, P.N.; Jha, D.K. Plant growth-promoting rhizobacteria (PGPR): Emergence in agriculture. *World J. Microbiol. Biotechnol.* **2012**, *28*, 1327–1350. https://doi.org/10.1007/s11274-011-0979-9.
42. Jalmi, S.K.; Sinha, A.K. Ambiguities of PGPR-Induced Plant Signaling and Stress Management. *Front. Microbiol.* **2022**, *13*, 899563. https://doi.org/10.3389/fmicb.2022.899563.
43. Kumari, R.; Pandey, E.; Bushra, S.; Faizan, S.; Pandey, S. Plant Growth Promoting Rhizobacteria (PGPR) induced protection: A plant immunity perspective. *Physiol. Plant.* **2024**, *176*, e14495. https://doi.org/10.1111/ppl.14495.
44. Afzal, I.; Shinwari, Z.K.; Sikandar, S.; Shahzad, S. Plant beneficial endophytic bacteria: Mechanisms, diversity, host range and genetic determinants. *Microbiol. Res.* **2019**, *221*, 36–49. https://doi.org/10.1016/j.micres.2019.02.001.
45. Ahirwar, N.K.; Gupta, G.; Singh, V.; Rawlley, R.K.; Ramana, S. Influence on growth and fruit yield of tomato (*Lycopersicon esculentum* Mill.) plants by inoculation with *Pseudomonas fluorescence* (SS5): Possible role of plant growth promotion. *Int. J. Curr. Microbiol. Appl. Sci.* **2015**, *4*, 720–730.
46. Andreolli, M.; Zapparoli, G.; Angelini, E.; Lucchetta, G.; Lampis, S.; Vallini, G. *Pseudomonas protegens* MP12: A plant growth-promoting endophytic bacterium with broad-spectrum antifungal activity against grapevine phytopathogens. *Microbiol. Res.* **2019**, *219*, 123–131. https://doi.org/10.1016/j.micres.2018.11.003.
47. Hol, W.H.G.; Bezemer, T.M.; Biere, A. Getting the ecology into interactions between plants and the plant growth-promoting bacterium *Pseudomonas fluorescens*. *Front. Plant Sci.* **2013**, *4*, 81. https://doi.org/10.3389/fpls.2013.00081.
48. Mhatre, P.H.; Karthik, C.; Kadirvelu, K.; Divya, K.L.; Venkatasalam, E.P.; Srinivasan, S.; Ramkumar, G.; Saranya, C.; Shanmuganathan, R. Plant growth promoting rhizobacteria (PGPR): A potential alternative tool for nematodes bio-control. *Biocatal. Agric. Biotechnol.* **2019**, *17*, 119–128. https://doi.org/10.1016/j.bcab.2018.11.009.
49. Pereira, R.V.; Filgueiras, C.C.; Dória, J.; Peñaflor, M.F.G.V.; Willett, D.S. The Effects of Biostimulants on Induced Plant Defense. *Front. Agron.* **2021**, *3*, 630596. https://doi.org/10.3389/fagro.2021.630596.
50. Ramamoorthy, V.; Viswanathan, R.; Raguchander, T.; Prakasam, V.; Samiyappan, R. Induction of systemic resistance by plant growth promoting rhizobacteria in crop plants against pests and diseases. *Crop Prot.* **2001**, *20*, 1–11. https://doi.org/10.1016/S0261-2194(00)00056-9.
51. Ramette, A.; Frapolli, M.; Saux, M.F.-L.; Gruffaz, C.; Meyer, J.-M.; Défago, G.; Sutra, L.; Moënne-Loccoz, Y. *Pseudomonas protegens* sp. nov., widespread plant-protecting bacteria producing the biocontrol compounds 2,4-diacetylphloroglucinol and pyoluteorin. *Syst. Appl. Microbiol.* **2011**, *34*, 180–188. https://doi.org/10.1016/j.syapm.2010.10.005.
52. Rasmann, S.; Bennett, A.; Biere, A.; Karley, A.; Guerrieri, E. Root symbionts: Powerful drivers of plant above- and belowground indirect defenses: *Root symbionts* and indirect defenses. *Insect Sci.* **2017**, *24*, 947–960. https://doi.org/10.1111/1744-7917.12464.
53. Ruiu, L. Plant-Growth-Promoting Bacteria (PGPB) Against Insects and Other Agricultural Pests. *Agronomy* **2020**, *10*, 861. https://doi.org/10.3390/agronomy10060861.
54. Ryan, R.P.; Germaine, K.; Franks, A.; Ryan, D.J.; Dowling, D.N. Bacterial endophytes: Recent developments and applications. *FEMS Microbiol. Lett.* **2008**, *278*, 1–9. https://doi.org/10.1111/j.1574-6968.2007.00918.x.

55. Grobelak, A.; Kokot, P.; Hutchison, D.; Grosser, A.; Kacprzak, M. Plant growth-promoting rhizobacteria as an alternative to mineral fertilizers in assisted bioremediation—Sustainable land and waste management. *J. Environ. Manag.* **2018**, *227*, 1–9. https://doi.org/10.1016/j.jenvman.2018.08.075.
56. Bukhat, S.; Imran, A.; Javaid, S.; Shahid, M.; Majeed, A.; Naqqash, T. Communication of plants with microbial world: Exploring the regulatory networks for PGPR mediated defense signaling. *Microbiol. Res.* **2020**, *238*, 126486. https://doi.org/10.1016/j.micres.2020.126486.
57. Majeed, A.; Kaleem Abbasi, M.; Hameed, S.; Yasmin, S.; Hanif, M.K.; Naqqash, T.; Imran, A. *Pseudomonas* sp. AF-54 containing multiple plant beneficial traits acts as growth enhancer of *Helianthus annuus* L. under reduced fertilizer input. *Microbiol. Res.* **2018**, *216*, 56–69. https://doi.org/10.1016/j.micres.2018.08.006.
58. Flury, P.; Aellen, N.; Ruffner, B.; Péchy-Tarr, M.; Fataar, S.; Metla, Z.; Dominguez-Ferreras, A.; Bloemberg, G.; Frey, J.; Goesmann, A.; et al. Insect pathogenicity in plant-beneficial pseudomonads: Phylogenetic distribution and comparative genomics. *ISME J.* **2016**, *10*, 2527–2542. https://doi.org/10.1038/ismej.2016.5.
59. Ali, S.; Moon, Y.-S. Advances in PGPR-Mediated Plant-Pathogen Control for Food Security and Ecosystem Stability. *Phyton* **2025**, *94*, 1419–1451. https://doi.org/10.32604/phyton.2025.064284.
60. Garrido-Sanz, D.; Meier-Kolthoff, J.P.; Göker, M.; Martín, M.; Rivilla, R.; Redondo-Nieto, M. Genomic and Genetic Diversity Within the *Pseudomonas fluorescens* Complex. *PLoS ONE* **2016**, *11*, e0150183. https://doi.org/10.1371/journal.pone.0150183.
61. Tovi, N.; Frenk, S.; Hadar, Y.; Minz, D. Host Specificity and Spatial Distribution Preference of Three Pseudomonas Isolates. *Front. Microbiol.* **2019**, *9*, 3263. https://doi.org/10.3389/fmicb.2018.03263.
62. Péchy-Tarr, M.; Bruck, D.J.; Maurhofer, M.; Fischer, E.; Vogne, C.; Henkels, M.D.; Donahue, K.M.; Grunder, J.; Loper, J.E.; Keel, C. Molecular analysis of a novel gene cluster encoding an insect toxin in plant-associated strains of *Pseudomonas fluorescens*. *Environ. Microbiol.* **2008**, *10*, 2368–2386. https://doi.org/10.1111/j.1462-2920.2008.01662.x.
63. Vesga, P.; Flury, P.; Vacheron, J.; Keel, C.; Croll, D.; Maurhofer, M. Transcriptome plasticity underlying plant root colonization and insect invasion by *Pseudomonas protegens*. *ISME J.* **2020**, *14*, 2766–2782. https://doi.org/10.1038/s41396-020-0729-9.
64. Kupferschmied, P.; Péchy-Tarr, M.; Imperiali, N.; Maurhofer, M.; Keel, C. Domain Shuffling in a Sensor Protein Contributed to the Evolution of Insect Pathogenicity in Plant-Beneficial *Pseudomonas protegens*. *PLoS Pathog.* **2014**, *10*, e1003964. https://doi.org/10.1371/journal.ppat.1003964.
65. Kupferschmied, P.; Maurhofer, M.; Keel, C. Promise for plant pest control: Root-associated pseudomonads with insecticidal activities. *Front. Plant Sci.* **2013**, *4*, 287. https://doi.org/10.3389/fpls.2013.00287.
66. Vesga, P.; Augustiny, E.; Keel, C.; Maurhofer, M.; Vacheron, J. Phylogenetically closely related pseudomonads isolated from arthropods exhibit differential insect-killing abilities and genetic variations in insecticidal factors. *Environ. Microbiol.* **2021**, *23*, 5378–5394. https://doi.org/10.1111/1462-2920.15623.
67. Aujoulat, F.; Pagès, S.; Masnou, A.; Emboulé, L.; Teyssier, C.; Marchandin, H.; Gaudriault, S.; Givaudan, A.; Jumas-Bilak, E. The population structure of *Ochrobactrum* isolated from *Entomopathogenic nematodes* indicates interactions with the symbiotic system. *Infect. Genet. Evol.* **2019**, *70*, 131–139. https://doi.org/10.1016/j.meegid.2019.02.016.
68. Flury, P.; Vesga, P.; Dominguez-Ferreras, A.; Tinguely, C.; Ullrich, C.I.; Kleespies, R.G.; Keel, C.; Maurhofer, M. Persistence of root-colonizing *Pseudomonas protegens* in herbivorous insects throughout different developmental stages and dispersal to new host plants. *ISME J.* **2019**, *13*, 860–872. https://doi.org/10.1038/s41396-018-0317-4.
69. Loper, J.E.; Hassan, K.A.; Mavrodi, D.V.; Davis, E.W.; Lim, C.K.; Shaffer, B.T.; Elbourne, L.D.H.; Stockwell, V.O.; Hartney, S.L.; Breakwell, K.; et al. Comparative Genomics of Plant-Associated *Pseudomonas* spp.: Insights into Diversity and Inheritance of Traits Involved in Multitrophic Interactions. *PLoS Genet.* **2012**, *8*, e1002784. https://doi.org/10.1371/journal.pgen.1002784.
70. Paulsen, I.T.; Press, C.M.; Ravel, J.; Kobayashi, D.Y.; Myers, G.S.A.; Mavrodi, D.V.; DeBoy, R.T.; Seshadri, R.; Ren, Q.; Madupu, R.; et al. Complete genome sequence of the plant commensal *Pseudomonas fluorescens* Pf-5. *Nat. Biotechnol.* **2005**, *23*, 873–878. https://doi.org/10.1038/nbt1110.
71. Dominelli, N. Adaptation and Regulation of the Alternative Lifestyle of Insect Pathogenic *Photorhabdus luminescens* in the Soil and its Potential as Biocontrol Agent. 2022. Available online: https://openscience.ub.uni-mainz.de/handle/20.500.12030/7270 (accessed on 12 June 2025).
72. Regaiolo, A.; Dominelli, N.; Andresen, K.; Heermann, R. The Biocontrol Agent and Insect Pathogen *Photorhabdus luminescens* Interacts with Plant Roots. *Appl. Environ. Microbiol.* **2020**, *86*, e00891-20. https://doi.org/10.1128/AEM.00891-20.
73. Helmberger, M.S.; Shields, E.J.; Wickings, K.G. Ecology of belowground biological control: Entomopathogenic nematode interactions with soil biota. *Appl. Soil Ecol.* **2017**, *121*, 201–213. https://doi.org/10.1016/j.apsoil.2017.10.013.

74. Park, Y.-S.; Ryu, C.-M. Understanding Plant Social Networking System: Avoiding Deleterious Microbiota but Calling Beneficials. *Int. J. Mol. Sci.* **2021**, *22*, 3319. https://doi.org/10.3390/ijms22073319.
75. Afridi, M.S.; Fakhar, A.; Kumar, A.; Ali, S.; Medeiros, F.H.V.; Muneer, M.A.; Ali, H.; Saleem, M. Harnessing microbial multitrophic interactions for rhizosphere microbiome engineering. *Microbiol. Res.* **2022**, *265*, 127199. https://doi.org/10.1016/j.micres.2022.127199.
76. Ansari, M.; Devi, B.M.; Sarkar, A.; Chattopadhyay, A.; Satnami, L.; Balu, P.; Choudhary, M.; Shahid, M.A.; Jailani, A.A.K. Microbial Exudates as Biostimulants: Role in Plant Growth Promotion and Stress Mitigation. *J. Xenobiotics* **2023**, *13*, 572–603. https://doi.org/10.3390/jox13040037.
77. Martins, D.P.; Barros, M.T.; Pierobon, M.; Kandhavelu, M.; Lio', P.; Balasubramaniam, S. Computational Models for Trapping Ebola Virus Using Engineered Bacteria. *IEEE/ACM Trans. Comput. Biol. Bioinform.* **2018**, *15*, 2017–2027. https://doi.org/10.1109/TCBB.2018.2836430.
78. Awan, H.; Adve, R.S.; Wallbridge, N.; Plummer, C.; Eckford, A.W. Communication and Information Theory of Single Action Potential Signals in Plants. *IEEE Trans. NanoBiosci.* **2019**, *18*, 61–73. https://doi.org/10.1109/TNB.2018.2880924.
79. Li, J.; Convertino, M. Inferring ecosystem networks as information flows. *Sci. Rep.* **2021**, *11*, 7094. https://doi.org/10.1038/s41598-021-86476-9.
80. Bi, D.; Almpanis, A.; Noel, A.; Deng, Y.; Schober, R. A Survey of Molecular Communication in Cell Biology: Establishing a New Hierarchy for Interdisciplinary Applications. *IEEE Commun. Surv. Tutor.* **2021**, *23*, 1494–1545. https://doi.org/10.1109/COMST.2021.3066117.
81. Unluturk, B.D.; Akyildiz, I.F. An End-to-End Model of Plant Pheromone Channel for Long Range Molecular Communication. *IEEE Trans. NanoBiosci.* **2017**, *16*, 11–20. https://doi.org/10.1109/TNB.2016.2628047.
82. Soheilypour, M.; Mofrad, M.R.K. Agent-Based Modeling in Molecular Systems Biology. *BioEssays* **2018**, *40*, 1800020. https://doi.org/10.1002/bies.201800020.
83. Le, D.-H.; Kwon, Y.-K. A coherent feedforward loop design principle to sustain robustness of biological networks. *Bioinformatics* **2013**, *29*, 630–637. https://doi.org/10.1093/bioinformatics/btt026.
84. Azeloglu, E.U.; Iyengar, R. Good practices for building dynamical models in systems biology. *Sci. Signal.* **2015**, *8*, fs8. https://doi.org/10.1126/scisignal.aab0880.
85. Pineda, A.; Zheng, S.-J.; van Loon, J.J.; Pieterse, C.M.J.; Dicke, M. Helping plants to deal with insects: The role of beneficial soil-borne microbes. *Trends Plant Sci.* **2010**, *15*, 507–514. https://doi.org/10.1016/j.tplants.2010.05.007.
86. Zhan, J.; Gurung, S.; Parsa, S.P.K. Identification of top-K nodes in large networks using Katz centrality. *J. Big Data* **2017**, *4*, 16. https://doi.org/10.1186/s40537-017-0076-5.
87. Dray, K.E.; Edelstein, H.I.; Dreyer, K.S.; Leonard, J.N. Control of mammalian cell-based devices with genetic programming. *Curr. Opin. Syst. Biol.* **2021**, *28*, 100372. https://doi.org/10.1016/j.coisb.2021.100372.
88. Ortiz-Romero, N.; Ochoa-Martínez, L.A.; González-Herrera, S.M.; Rutiaga-Quiñones, O.M.; Gallegos-Infante, J.A. Avances en las investigaciones sobre la encapsulación mediante gelación iónica: Una revisión sistemática. *TecnoLógicas* **2021**, *24*, e1962. https://doi.org/10.22430/22565337.1962.
89. Thakur, S.; Sharma, B.; Verma, A.; Chaudhary, J.; Tamulevicius, S.; Thakur, V.K. Recent progress in sodium alginate based sustainable hydrogels for environmental applications. *J. Clean. Prod.* **2018**, *198*, 143–159. https://doi.org/10.1016/j.jclepro.2018.06.259.
90. Lee, K.Y.; Mooney, D.J. Alginate: Properties and biomedical applications. *Prog. Polym. Sci.* **2012**, *37*, 106–126. https://doi.org/10.1016/j.progpolymsci.2011.06.003.
91. Riseh, R.S.; Tamanadar, E.; Pour, M.M.; Thakur, V.K. Novel Approaches for Encapsulation of Plant Probiotic Bacteria with Sustainable Polymer Gums: Application in the Management of Pests and Diseases. *Adv. Polym. Technol.* **2022**, *2022*, 4419409. https://doi.org/10.1155/2022/4419409.
92. Rojas-Sánchez, B.; Guzmán-Guzmán, P.; Morales-Cedeño, L.R.; Orozco-Mosqueda, M.d.C.; Saucedo-Martínez, B.C.; Sánchez-Yáñez, J.M.; Fadiji, A.E.; Babalola, O.O.; Glick, B.R.; Santoyo, G. Bioencapsulation of Microbial Inoculants: Mechanisms, Formulation Types and Application Techniques. *Appl. Biosci.* **2022**, *1*, 198–220. https://doi.org/10.3390/applbiosci1020013.
93. Saberi Riseh, R.; Skorik, Y.A.; Thakur, V.K.; Moradi Pour, M.; Tamanadar, E.; Noghabi, S.S. Encapsulation of Plant Biocontrol Bacteria with Alginate as a Main Polymer Material. *Int. J. Mol. Sci.* **2021**, *22*, 11165. https://doi.org/10.3390/ijms222011165.
94. Balla, A.; Silini, A.; Cherif-Silini, H.; Chenari Bouket, A.; Alenezi, F.N.; Belbahri, L. Recent Advances in Encapsulation Techniques of Plant Growth-Promoting Microorganisms and Their Prospects in the Sustainable Agriculture. *Appl. Sci.* **2022**, *12*, 9020. https://doi.org/10.3390/app12189020.
95. Vargas, P.O.; Pereira, N.R.; Guimarães, A.O.; Waldman, W.R.; Pereira, V.R. Shrinkage and deformation during convective drying of calcium alginate. *LWT* **2018**, *97*, 213–222. https://doi.org/10.1016/j.lwt.2018.06.056.

96. Saberi-Riseh, R.; Moradi-Pour, M.; Mohammadinejad, R.; Thakur, V.K. Biopolymers for Biological Control of Plant Pathogens: Advances in Microencapsulation of Beneficial Microorganisms. *Polymers* **2021**, *13*, 1938. https://doi.org/10.3390/polym13121938.
97. Saberi Riseh, R.; Hassanisaadi, M.; Vatankhah, M.; Kennedy, J.F. Encapsulating biocontrol bacteria with starch as a safe and edible biopolymer to alleviate plant diseases: A review. *Carbohydr. Polym.* **2023**, *302*, 120384. https://doi.org/10.1016/j.carbpol.2022.120384.
98. Kim, J.; Hiltpold, I.; Jaffuel, G.; Sbaiti, I.; Hibbard, B.E.; Turlings, T.C.J. Calcium-alginate beads as a formulation for the application of *Entomopathogenic nematodes* to control rootworms. *J. Pest Sci.* **2021**, *94*, 1197–1208. https://doi.org/10.1007/s10340-021-01349-4.
99. Cruz-Martínez, H.; Ruiz-Vega, J.; Matadamas-Ortíz, P.T.; Cortés-Martínez, C.I.; Rosas-Diaz, J. Formulation of *Entomopathogenic nematodes* for crop pest control—A review. *Plant Prot. Sci.* **2017**, *53*, 15–24. https://doi.org/10.17221/35/2016-PPS.
100. Gaugler, R.; Lewis, E.; Stuart, R.J. Ecology in the service of biological control: The case of *Entomopathogenic nematodes*. *Oecologia* **1997**, *109*, 483–489. https://doi.org/10.1007/s004420050108.
101. Pour, M.M.; Saberi-Riseh, R.; Mohammadinejad, R.; Hosseini, A. Investigating the formulation of alginate-gelatin encapsulated *Pseudomonas fluorescens* (VUPF5 and T17-4 strains) for controlling *Fusarium solani* on potato. *Int. J. Biol. Macromol.* **2019**, *133*, 603–613. https://doi.org/10.1016/j.ijbiomac.2019.04.071.
102. Panichikkal, J.; Prathap, G.; Nair, R.A.; Krishnankutty, R.E. Evaluation of plant probiotic performance of *Pseudomonas* sp. encapsulated in alginate supplemented with salicylic acid and zinc oxide nanoparticles. *Int. J. Biol. Macromol.* **2021**, *166*, 138–143. https://doi.org/10.1016/j.ijbiomac.2020.10.110.
103. Vejan, P.; Khadiran, T.; Abdullah, R.; Ismail, S.; Dadrasnia, A. Encapsulation of plant growth promoting Rhizobacteria—Prospects and potential in agricultural sector: A review. *J. Plant Nutr.* **2019**, *42*, 2600–2623. https://doi.org/10.1080/01904167.2019.1659330.
104. Kaya, H.K.; Nelsen, C.E. Encapsulation of *Steinernematid* and *Heterorhabditid nematodes* with Calcium Alginate: A New Approach for Insect Control and Other Applications. *Environ. Entomol.* **1985**, *14*, 572–574. https://doi.org/10.1093/ee/14.5.572.
105. Hiltpold, I.; Hibbard, B.E.; French, B.W.; Turlings, T.C.J. Capsules containing *Entomopathogenic nematodes* as a Trojan horse approach to control the western corn rootworm. *Plant Soil* **2012**, *358*, 11–25. https://doi.org/10.1007/s11104-012-1253-0.
106. Kim, J.; Jaffuel, G.; Turlings, T.C.J. Enhanced alginate capsule properties as a formulation of *Entomopathogenic nematodes*. *BioControl* **2015**, *60*, 527–535. https://doi.org/10.1007/s10526-014-9638-z.
107. Jaffuel, G.; Sbaiti, I.; Turlings, T.C.J. Encapsulated *Entomopathogenic nematodes* Can Protect Maize Plants from Diabrotica balteata Larvae. *Insects* **2019**, *11*, 27. https://doi.org/10.3390/insects11010027.
108. van Elsas, J.D.; Trevors, J.T.; Jain, D.; Wolters, A.C.; Heijnen, C.E.; van Overbeek, L.S. Survival of, and root colonization by, alginate-encapsulated *Pseudomonas fluorescens* cells following introduction into soil. *Biol. Fertil. Soils* **1992**, *14*, 14–22. https://doi.org/10.1007/BF00336297.
109. Russo, A.; Basaglia, M.; Tola, E.; Casella, S. Survival, root colonisation and biocontrol capacities of *Pseudomonas fluorescens* F113 LacZY in dry alginate microbeads. *J. Ind. Microbiol. Biotechnol.* **2001**, *27*, 337–342. https://doi.org/10.1038/sj.jim.7000154.
110. Heo, K.R.; Lee, K.Y.; Lee, S.H.; Jung, S.J.; Lee, S.W.; Moon, B.J. Control of Crisphead Lettuce Damping-off and Bottom Rot by Seed Coating with Alginate and *Pseudomonas aeruginosa* LY-11. *Plant Pathol. J.* **2008**, *24*, 67–73.
111. Power, B.; Liu, X.; Germaine, K.J.; Ryan, D.; Brazil, D.; Dowling, D.N. Alginate beads as a storage, delivery and containment system for genetically modified PCB degrader and PCB biosensor derivatives of *Pseudomonas fluorescens* F113: Alginate beads; a delivery system for GM PCB degrading Pseudomonas. *J. Appl. Microbiol.* **2011**, *110*, 1351–1358. https://doi.org/10.1111/j.1365-2672.2011.04993.x.